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RESEARCH ARTICLE

Perennial flower margins reduce orchard fruit damage by rosy apple aphid, *Dysaphis plantaginea* (Homoptera: Aphididae)

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Abstract

1. Sown or natural flower strips are a commonly used management practice in agro-ecosystems and have been demonstrated to increase the abundance of predators of orchard pests. There is less evidence of the extent to which such strips can reduce pest damage in orchards.
2. Here we examined the effect of managed, perennial flower margins on fruit damage by an economically significant crop pest, *Dysaphis plantaginea*, rosy apple aphid, in conventional apple orchards over 2 years, compared to orchards without flower margins.
3. We found orchard flower margins reduced the percentage of apple trees with fruit damage by *D. plantaginea*, from 80% to 48%. In 2021, a period of severe infestation (65% of trees had fruit damage), there was reduced spread of *D. plantaginea* on infested apple trees and the number of trees with fruit damage was significantly reduced up to 50 m into orchards. During 2022, a period of lower infestation (25% of trees damaged), fruit damage was significantly reduced up to 10 m from the flower margin.
4. A significant reduction in predation of aphids from bait cards in flower margin compared with control orchards suggests specialists, rather than generalist predators, may be driving the positive effects of the margin on pest pressure. There was no significant effect of flower margins on abundance of important aphid predators, including Syrphidae (hoverflies) and Coccinellidae (ladybirds).
5. *Synthesis and applications*: To our knowledge, this study is the first to detect a reduction in fruit damage by pests at harvest in orchards with a flower margin. We highlight the potential for established perennial flower margins to deliver measurable, sustainable, *D. plantaginea* control benefits and provide insights into the optimal spatial arrangement of flower strips in orchards.

KEYWORDS
apple production, conventional management, ecosystem services, integrated pest management, natural enemy, pest control, predator

1 | INTRODUCTION

Loss of key resources and habitats in agricultural landscapes can have negative impacts on biodiversity and species beneficial to ecosystem services (Emmerson et al., 2016). Sown or natural flower strips are one of the more commonly used management practices designed to support the natural predators and parasites of crop pests (natural enemies) (Herz et al., 2019). They can be sown within the crop or border the crop as a margin. It has been reported that a mix of perennial wildflowers, in particular, can provide beneficial insects with breeding and/or food resources year-round, and from year-to-year (Fountain, 2022 and references therein). A recent meta-analysis exploring the use of flower margins found they lead to increased abundance and diversity of arthropod and natural enemy communities within the margin and in adjacent crops (Crowther et al., 2023). The same analysis also showed that sown margins, and to a lesser extent, spontaneous vegetation, reduced pest abundance in comparison to grass control margins (Crowther et al., 2023). Supporting natural enemies through such approaches can reduce reliance on chemical pest control (Cahenzli et al., 2017; Dib, Sauphanor, & Capowiez, 2016; Judt et al., 2023).

Apple is one of the most widely grown fruits in the world, with 93 million tonnes harvested in 2021 (Food and Agricultural Organization, 2023). In 2020, the UK produced 200 thousand tonnes of dessert apples with a value of £158 million (DEFRA (Department for Environment, Food, & Rural Affairs), 2020). Dessert apple production requires intensive management typically involving high inputs of pesticides and fertiliser (Herz et al., 2019; Simon, Bouvier, et al., 2011; Simon, Brun, et al., 2011). Even organic production requires regular use of biological and organic plant protection products to obtain a reliable and economically viable yield (Daniel et al., 2018). Hence, there is particular interest in the use of flower margins as a biocontrol strategy.

Rosy apple aphid, *Dysaphis plantaginea* (Passerini), is an important apple pest which can cause significant economic damage, even at low population levels, such as leaf curling, reduction of fruit size and fruit deformation (Blommers et al., 2004). If untreated, *D. plantaginea* infestation can lead to economic losses of up to 80% (C. Schulz, 2003, pers. comm. in Qubbaj et al., 2005), and hence aphid infestations in fruit orchards are typically treated using insecticides (Dib et al., 2010; Penvern et al., 2010). Whilst insecticides can be an affordable and effective part of integrated pest management (IPM), the drawbacks can include pesticide resistance (Dunley & Welter, 2000; Pretty et al., 2018) and biodiversity loss (Katayama et al., 2019), including negative effects on non-target organisms such as pollinators (Goulson et al., 2015) and natural enemies (Fountain & Harris, 2015). The use and availability of pesticides changes over time (McKerchar et al., 2020), and recent pesticide withdrawals are leaving fruit growers with fewer effective products (Cressey, 2017). Studies have demonstrated that aphids can be suppressed by natural enemies (Dib et al., 2010) including generalist predators, such as earwigs and spiders (Dib et al., 2010; Diehl et al., 2013) and specialists including Syrphidae (hoverfly) larvae, Coccinellidae (ladybirds), Chryopsidae (lacewings) larvae and parasitoid wasps (Order: Hymenoptera) (Dib et al., 2010; Graham, 1989; Solomon et al., 2000). Predacious bugs (Anthocoridae, Miridae and Nabidae) and predacious beetles (Cantharidae and Staphylinidae) are also aphidophagous (Dib et al., 2010; Dib, Jamont, et al., 2016). Additionally, Formicidae (ants) can predate aphids, but in the absence of sugar resources such as nectar, they form mutualisms whereby they protect aphids from predators in return for the sugars they excrete (Nagy et al., 2015). These natural enemy groups often rely on floral resources for food during various life-stages or scarcity of aphid prey (Markó et al., 2013; Wyss, 1995).

Whilst there is evidence for increased abundance and diversity of natural enemies in apple orchards with flower strips, there is a lack of evidence of increased pest control services such as increased yield (Fountain, 2022; Herz et al., 2019), as is true for crops generally (Crowther et al., 2023). For example, only a few studies have investigated apple damage, most finding no effect (Cahenzli et al., 2019; Campbell et al., 2017; Jacobsen et al., 2022). Additionally, many studies to date have been in organic or insecticide-free orchards, with fewer in orchards using Integrated Pest Management (Fountain, 2022).

The spatial extent of the effect of flower strips to control pests into orchards (spill-over) is also uncertain. Benefits have been found only in close proximity, such as the row of apples neighbouring the flowers (Albert et al., 2017; Cahenzli et al., 2019; Jacobsen et al., 2022). Studies for crops in general, apples included, suggest that positive effects can extend to 50 m for generalist natural enemies (Woodcock et al., 2016; Wyss et al., 1995) with the effects decreasing with increasing distance from the flower strip (Albert et al., 2017; Collins et al., 2002; Gontijo et al., 2013; Mei et al., 2021; Tylianakis et al., 2004). The effects of perennial flower strips on fruit damage specifically have more often been investigated with alleyway flower strips and trees in close proximity (up to 3 rows away) rather than investigating the effects of flower margins on more distant trees. More knowledge on the spill-over effects of well-established flower margins in orchards is needed for fruit growers designing orchards and landscapes for more effective ecosystem service delivery.

This study aimed to examine the spatial effect of established perennial flower margins on pest pressure and fruit damage by *D. plantaginea*. The objectives were to (1) determine whether flower margins can suppress *D. plantaginea* and subsequent fruit damage in conventionally managed apple orchards; (2) establish whether this is driven by the abundance and activity of natural enemies in the orchard trees; and (3) quantify the distance of spill-over from flower margins into orchards. We hypothesised that predator abundance and predation would be increased in orchards with adjacent flower margins, leading to overall reduced aphid pressure and fruit damage, particularly close to the flower margin.

2 | MATERIALS AND METHODS

2.1 | Study sites

Gala is the most widespread variety of dessert apple grown in the UK (DEFRA (Department for Environment, Food, & Rural Affairs), 2020). This study took place in 10 commercial dessert apple orchards (Gala var.) located in Kent, UK (Appendix A). Five orchards, termed 'flower margin orchards' were bordered by an established sown perennial flower margin (2–5 years), and five 'control orchards' had only a permanent grass headland 4–5 m wide, typically mown four times a year (Figure 1, Figure S1). The average width of the flower margins was 15 m (SD = 9.6 m) (Table S1). All orchards were conventionally managed, involving the use of aphicides such as Flonicamid, Spirotetramat and Acetamiprid. The flower margin and control orchards were paired on the same farm so that the use of pesticides, nutrients and mowing was consistent, with a distance of 120–410 m between treatments to minimise co-use by the same invertebrates and differences in soil type and aspect.

2.2 | Flower margins

Four of the flower margins were sown in 2017 with four low-growing fine grass species and 15 perennial flowering species designed to offer multiple flowering times and flower shapes and maximise pollen and nectar resources (Table S2; Carvell et al., 2022). At the fifth site, the margin was sown in 2019 with a different perennial seed

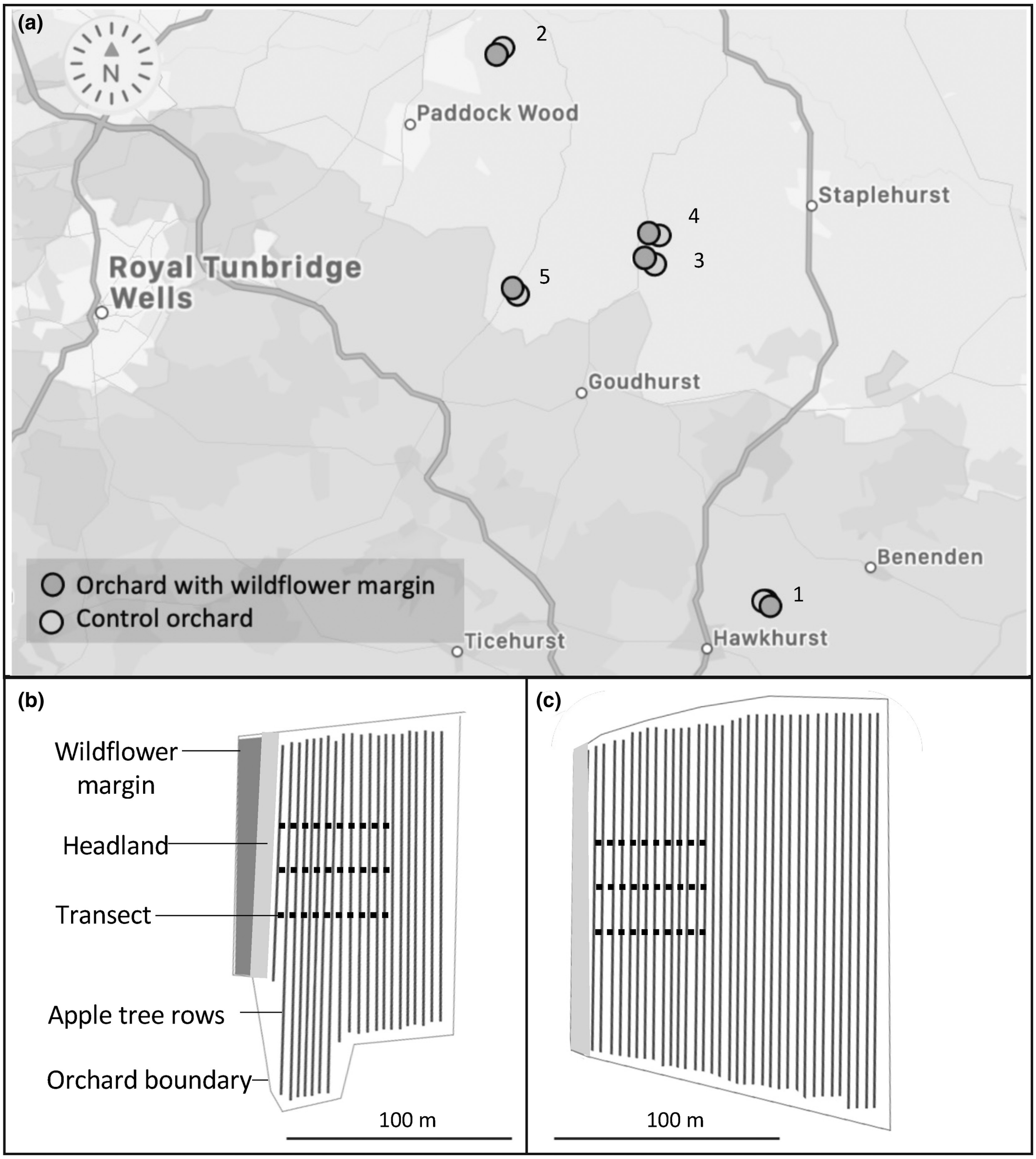

FIGURE 1 Map showing locations of the 10 study orchards in Kent, South East England, UK, numbered according to orchard pair (a) (Taken from Apple Maps), typical layout of an orchard with a flower margin (b) and without (control) (c) (Adapted from Carvell et al., 2022; Appendix A.1).

mix with some overlap of the plant species (Table S2). To encourage earlier flowering, and to keep weeds under control, all flower margins were cut to 8–10 cm annually in autumn and the cuttings were removed (Carvell et al., 2022). They did not receive fertiliser or herbicide treatments.

2.3 | Sampling design

Data were collected along three 50 m transects extending from the flower margin or control edge to the centre of each orchard. Transects were 20 m apart, and to reduce edge effects, at least 20 m from the perpendicular field edge (Figure 1). Flower margin and control edges were matched for adjacent habitat types, ordinal direction and tree row direction where possible. Where it was not possible to meet all criteria, priority was given to matching the adjacent habitat (including type of crop and type of semi-natural habitat). In the narrowest orchard, 50 m was the furthest into the orchard that could be sampled before becoming closer to the opposite edge and so was set as the maximum distance. Five distances along each transect were chosen for sampling: 0, 5, 10, 20 and 50 m. Generally, a distance of 5 m and 10 m from the edge corresponded with tree rows 2 and 4, respectively, so for consistency, data were collected from these rows in each orchard and then from a row at least 20 and 50 m from the orchard edge.

2.4 | Aphid assessments

Abundance of *D. plantaginea* was assessed at three-week intervals from April to July in 2021 and 2022 during the apple-growing season, after which *D. plantaginea* typically migrates to a secondary host, plantain (*Plantago* spp.). This included a pre-bloom assessment in April, an assessment during bloom in May, and post-bloom assessments during the fruitlet and fruit stages in July and August. For each of the three transects, three trees were surveyed at each of the five distances (45 trees per orchard). Ten areas on one side of each tree were searched for the presence of *D. plantaginea* on buds, flower clusters with leaves, rosettes of leaves, long shoots and fruitlet clusters (tree areas), depending on the phenological stage of the tree (Cahenzli et al., 2019; Figure 2). To cover a range of areas on the tree, areas were searched systematically, starting next to the trunk on the lowest branch on the right and finishing with the highest reachable branch on the left (up to 2 m), and searching areas in-between in an arc across the tree (Figure 2), alternating the position of the branch between proximal, distal and intermediate distance from the trunk. Curled leaves were uncurled to search inside. The number of *D. plantaginea* colonies were counted and the number of aphids in each was estimated. Natural enemy taxa including ants and aphid mummies (host to a pupated parasitoid wasp) were recorded. The active predatory stage of most predators of *D. plantaginea* is not highly dispersing, and as such, systematic visual searches were well-suited to sampling these groups (Araneae, predatory Hemiptera, Opilliones, Coccinellidae, Dermaptera, Syrphidae larvae and Neuroptera larvae). When present, natural enemies were identified in the field. Assessments and sampling were carried out between 08:00 and 18:30. Paired orchards were surveyed on the same day to minimise weather effects. The order of visits to each site was randomised.

2.5 | Aphid fruit damage assessment

The same three trees used for *D. plantaginea* assessments were assessed for pre-harvest fruit damage on each of the three transects, at each of the five transect distances. The total number of fruit and number of fruit with *D. plantaginea* damage was counted on each tree. Rosy apple aphid-damaged fruit was identified by reduced size, malformed shape, often with puckering around the calix (Figure 3) and/or a coating of aphid honeydew which can lead to sooty mould (Warren & Schalau, 2014). A pre-harvest thinning of fruit was carried out a few days before the fruit damage assessment in one of the five orchard pairs. In that case, pest-damaged fruits which had been removed from the tree and dropped to the ground below, were included in the calculation of total fruit number.

2.6 | Sentinel bait experiment

Sentinel bait cards (Boetzl et al., 2020) were deployed to assess predator activity in the trees in 2021. Since rosy apple aphids are not commercially available, a culture of *Acyrthosiphon pisum* (pea aphid) was obtained from Dartfrog (http://www.dartfrog.co.uk). Aphids were reared in vitro at room temperature on *Pisum sativum* (pea) and *Vicia faba* (broad bean) in cages (44.5 cm^3) of fine nylon mesh (160 µm mesh). Ten adult and late-stage *A. pisum* nymphs were euthanised in a freezer and then glued to a polyvinyl chloride card (Mateos-Fierro et al., 2021; Figure 4) which was hung adjacent to the trunk from the lowest branch of three apple trees at each of the five transect distances. The percentage of aphids depleted by predators and scavengers was recorded, where possible, every 48 h for 5 days in May, 6 days in July and 8 days in September, after deployment (Figure 7). This study did not require ethical approval, licences or permits.

2.7 | Statistical analyses

Statistical analyses were carried out in R 4.2.2 for Mac (R Core Team, 2022), using the lme4 package for mixed effect modelling (Bates et al., 2015).To account for the experimental design of nested repeated measures within a transect, orchard and pair of orchards, generalised linear mixed models (GLMM) were used. Binomial models were used for proportional data, and Poisson models (or negative binomials in the case of overdispersion) were

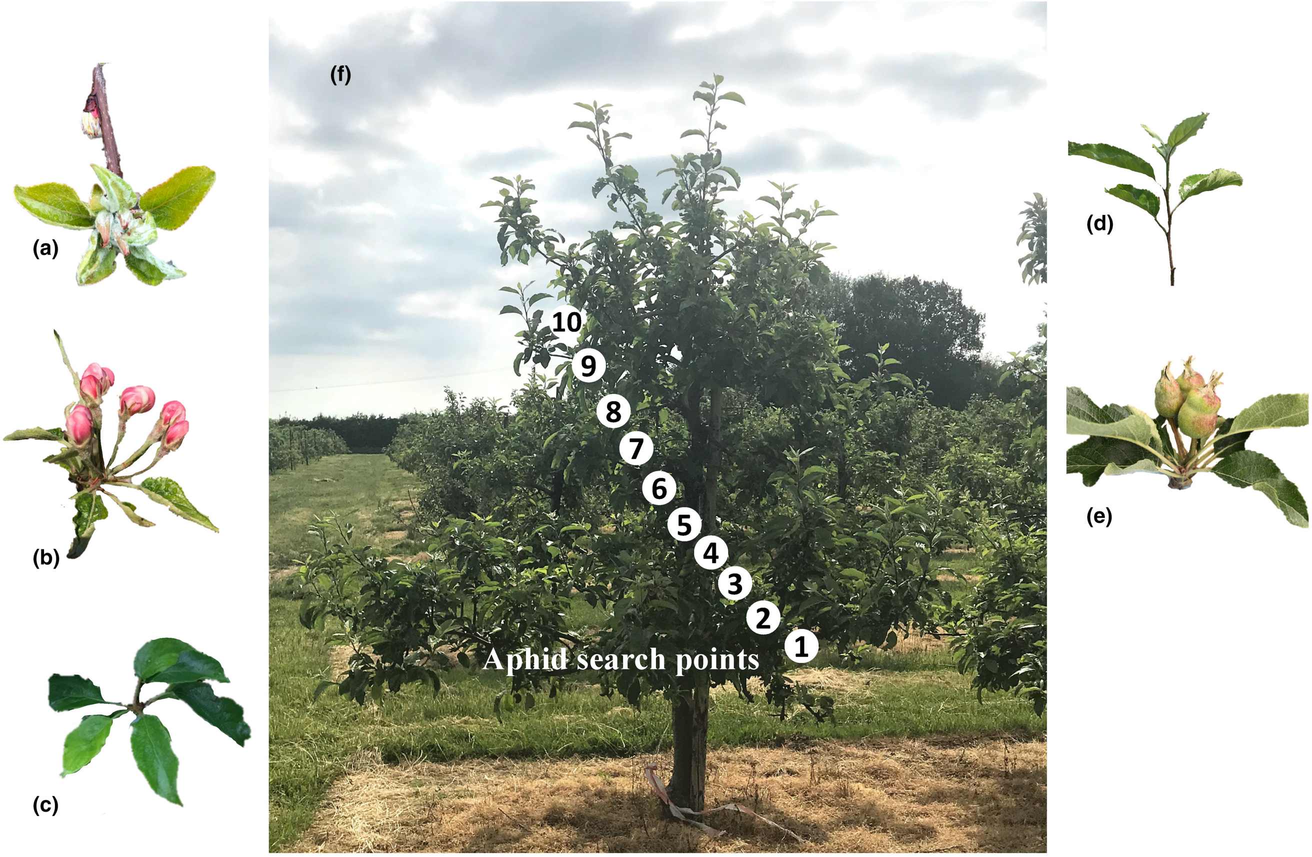

FIGURE 2 Areas (a–e) and positions (f) on commercial apple trees selected for visual searches for rosy apple aphids. Areas include (a) buds, (b) flower clusters with leaves, (c) rosettes of leaves, (d) long shoots and (e) fruit clusters.

FIGURE 3 Damage to apples by *Dysaphis plantaginea*, where fruits are reduced in size and malformed, with puckering around the calix (left) and *D. plantaginea*-damaged apples beneath a non-damaged, full-sized apple (right).

used for other data. The assumptions of the GLMM were tested, including linearity, response distribution, independence and multicollinearity of predictors. Models were also tested for overdispersion where appropriate. Aphid densities can be uneven due to their natural distribution, leading to data analysis issues such as overdispersion and zero inflation. To account for this, colony metrics, fruit damage and enemy abundance data were modelled using a hurdle (zero-adjusted) model (e.g. Sampaio et al., 2017), a two-step approach which evaluates the zero values using a binomial linear regression and then uses truncated linear regression for the positive values. Therefore, the data are considered first on a presence-absence basis (e.g. are trees aphid-infested or not), and

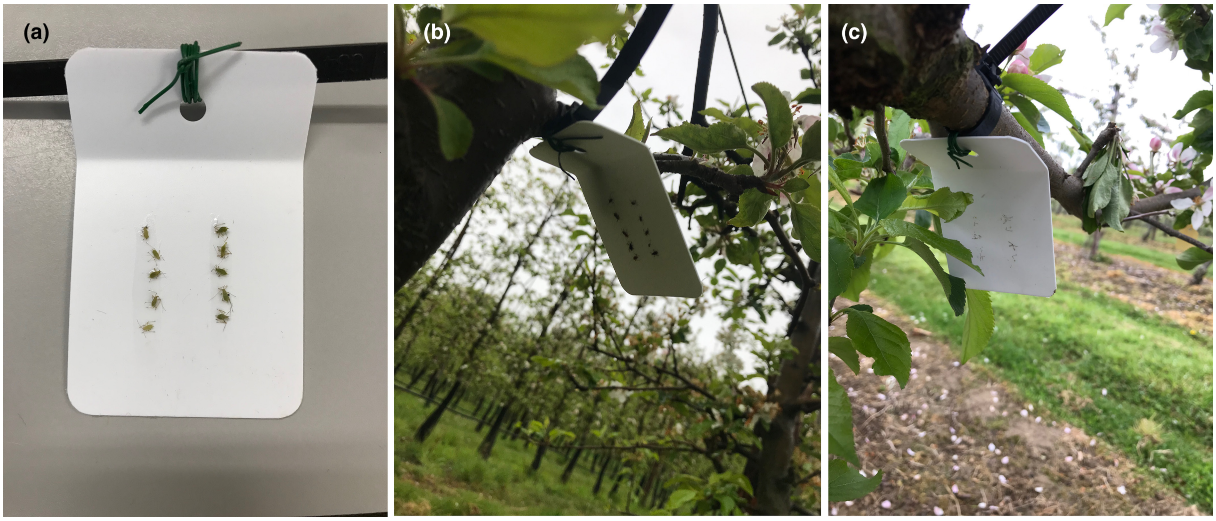

FIGURE 4 Sentinel bait card of (a) 10 adult and late-stage *Acyrthosiphon pisum* nymphs glued to a pvc card (as in Mateos-Fierro et al., 2021), (b) hung at approximately 1.5 m in the lowest apple tree branch and (c) depleted by predators and scavengers.

then the counts are assessed (e.g. abundance of aphids on infested trees) (Zuur et al., 2009). Tukey-adjusted multiple comparisons were used to identify the differences driving significant interactive model terms using the emmeans package (Lenth, 2023). Year was used as a fixed effect where possible, but separate models were created for each sampling year to aid model convergence where needed (Table 1). Similarly, sampling 'round' was included as a fixed effect where possible, but values were averaged across the year if needed (Table 1). The random effect structure had to be simplified in some cases to avoid over-fitting (Table 1). Total fruits per meter squared was modelled to compare productivity between flower margin and control orchards, accounting for differences in fruits per tree due to varying production systems affecting intra-row tree spacing and tree height.

3 | RESULTS

3.1 | Aphids

Between April and July 2021, *D. plantaginea* was present on 23% of 450 surveyed trees. Peak abundance was in June, with an average of 71 aphids per tree (all trees) (SD = 305 aphids). Across the 2021 season, there was no significant effect of the presence of a flower margin on the percentage of trees with *D. plantaginea* ($\chi^2 = 5.165$, df = 4, $p > 0.05$). However, infested trees had fewer aphid-infested areas in flower margin orchards compared with controls (Figure 5a; $\chi^2 = 17.924$, df = 1, $p < 0.001$). Overall, *D. plantaginea* presence was significantly reduced with increased distance from the orchard edge ($\chi^2 = 25.454$, df = 4, $p < 0.001$). There was also a significant interaction between distance and the presence of a flower margin ($\chi^2 = 12.188$, df = 4, $p < 0.01$), which meant that the flower margin was associated with fewer aphids per infested tree at 10 m into the orchard (*Z* ratio = 2.286, $p < 0.05$; Figure 5b), but not at other distances.

In 2022, *D. plantaginea* was only on 4.5% of 1799 tree searches across the season with a mean of 6% in flower margin and 3% in control orchards, although we could not test for significance. Only two aphid mummies were found across both seasons. In both cases, the numbers were too low for detailed statistical analysis.

3.2 | Aphid fruit damage

The percentage of trees with *D. plantaginea*-damaged fruit varied with year. The mean percentage of trees with *D. plantaginea*-damaged fruit was 65% in 2021 and 25% in 2022. There were significant interactions between treatment, distance from the orchard edge and year, on the probability of fruit damage on a tree (spread of damage within the orchard; Figure 6; $\chi^2 = 35.996$, df = 13, $p < 0.001$). Additionally, on those trees with damaged fruit, there were significant interactions between treatment, distance from the orchard edge and year, on the percentage of damaged fruit (intensity of damage on affected trees), detailed below (Figure 6; $\chi^2 = 137.65$, df = 13, $p < 0.001$).

In 2021, there was a mean of 93 (SD = 73) apples per tree across all 10 orchards. In 2021, orchards with flower margins had significantly fewer trees with fruit damage by *D. plantaginea* (48%) than control orchards (80%) overall (SD = 3; Figure 6a, Table S3). Orchards with flower margins had significantly fewer trees with fruit damage at all measured distances from the orchard edge (0–50 m; Figure 6c, Table S3). The mean percentage of *D. plantaginea*-damaged fruit on affected trees was 4.1% in the flower margins and 11.1% in the control orchards, although the effect was not significantly different (Table S3).

In 2022, there was, again, a mean of 93 (SD = 76) apples per tree across all 10 orchards. Orchards with a flower margin had significantly fewer trees with *D. plantaginea*-damaged fruit than control orchards, this time at 5 m and 10 m from the orchard edge (Figure 6b, Table S3). In general, in 2022, the mean percentage of *D. plantaginea*-damaged fruit on affected trees was similar in the flower margin

TABLE 1 Model building specifications, where a ● symbol indicates where fixed and random effects were applied to each response variable for (a) 2-part hurdle (zero-adjusted) models and (b) non-hurdle models.

				Fixed terms					Random terms			Weights
Response	Data	Sampling methods	Distribution	Treatment	Distance	Year	Round	Aphid[1] abundance *0.01	Pair	Orchard	Transect	No. aphids deployed[2]
(a) Fruit damage by Rosy apple aphids												
Presence/absence	All trees	Pre-harvest fruit damage assessment	Binomial	●	●	●			●	●		
Percentage (damaged&undamaged)	Affected trees	Pre-harvest fruit damage assessment	Binomial	●	●	●			●	●	●	
Apples per meter squared	All trees	Visual aphid assessments across the season	Negative binomial	●	●	●			●	●	●	
Aphid metrics in 2021 (averaged by round)												
Presence/absence	All trees	Visual aphid assessments across the season	Binomial	●	●				●			
Spread	Aphid-infested trees	Visual aphid assessments across the season	Binomial	●	●				●			
Abundance	Aphid-infested trees	Visual aphid assessments across the season	Poisson	●	●				●	●	●	
Syrphidae metrics during peak aphid abundance, June 2021												
Presence/absence	All trees	Visual aphid assessments across the season	Binomial	●	●			●	●	●		
Abundance	Aphid-infested trees	Visual aphid assessments across the season	Negative binomial	●	●			●	●			
Coccinellidae metrics during peak aphid abundance, June 2021												
Presence/absence	All trees	Visual aphid assessments across the season	Binomial	●	●			●	●	●	●	
Ant presence/absence, 2021	All trees	Visual aphid assessments across the season	Binomial	●			●	●	●	●		
(b) Percentage predation from bait cards after 5 to 8 days from deployment	All trees	Bait cards	Binomial	●	●		●		●	●	●	●

Note: 'Treatment' fixed effect refers to the presence or absence of a perennial flower margin. 'Pair' fixed effect refers to the experimental design whereby each treatment orchard is paired with a control orchard. Random effects were nested in the order in which they appear in the table.

[1] The total number of aphids per tree was appropriately scaled to match the other fixed effects in the model. This was done using a multiplication of 0.01.

[2] The model was weighted according to the number of aphids deployed to account for occasional cards with fewer than 10 aphids, for example, if one fell off during transit.

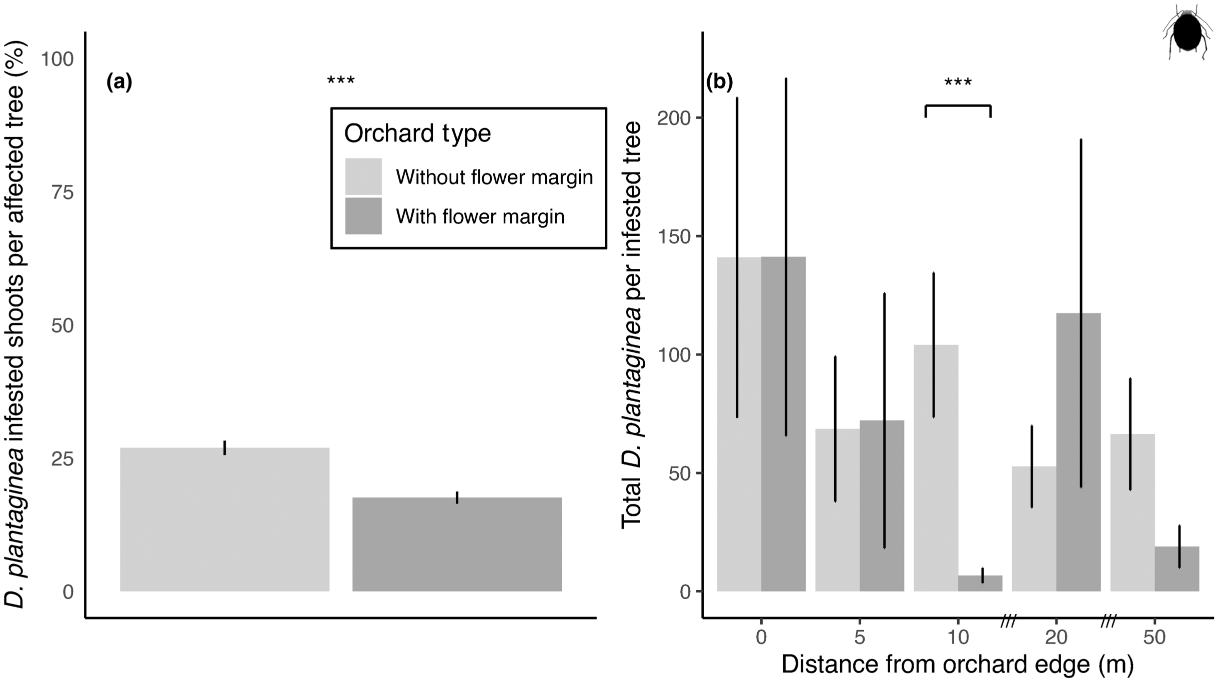

FIGURE 5 Effect of presence/absence of a flower margin on (a) the mean percentage of infested shoots per infested tree in 2021 and (b) the mean total number of *Dysaphis plantaginea* on apple trees in 2021 at distances from the orchard edge. Lines show standard error. Stars denote significance of treatment; $^*p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$.

(1.4%) and control orchards (1.5%), however only 1.5% of apples on affected trees were damaged (Figure 6d). In 2022, orchards with a flower margin had significantly higher percentage of *D. plantaginea*-damaged fruit on affected trees than control orchards at 50 m from the orchard edge.

Irrespective of fruit damage, across both years, there was no significant difference in total number of apples per square metre between flower margin and control orchards, year or distance from the orchard edge ($\chi^2=0.557$, df = 1, $p>0.05$ and $\chi^2=3.631$, df = 1, $p>0.05$ and $\chi^2=4.112$, df = 4, $p>0.05$, respectively).

3.3 | Sentinel bait cards

Depletion of *A. pisum* from bait cards was significantly lower in flower margin orchards compared with controls at 10, 20 and 50 m from the orchard edge in May, at 10 and 20 m in July and at 50 m in September 2021 and was significantly higher in flower margin orchards compared to controls at 0 m from the orchard edge in September (Figure 7, Table S5) (interaction: $\chi^2=19{,}153$, df = 22, $p<0.001$).

3.4 | Predators associated with *Dysaphis plantaginea* surveys

Combined across 2021 and 2022 aphid surveys, 668 natural enemies were counted in the apple trees, of which 61% were found in 2021 when *D. plantaginea* infestation was high. The following predator groups were recorded; Araneae (45%), Syrphidae (27%), Coccinellidae (21%), Heteroptera (10%), Forficulidae (1%), Chrysopidae (<1%), Opiliones (<1%) and *Aphidoletes aphidimyza* (Cecidomyiidae) (1%). The most abundant group, Araneae, comprising spiders, a generalist predator, was found across most sampling rounds albeit in consistently low numbers (too low for statistical modelling). In 2021, the mean number of spiders was one for every 20 trees and 25 trees (SD = 5 trees) in flower margin orchards and control orchards, respectively. In 2022, the mean number of spiders was one for every 10 (SD = 4) trees in orchards with and without a flower margin. Araneae and predator groups which represent 10% or less of the abundance of the total number of natural enemies were not considered for the subsequent statistical analyses.

The second most abundant natural enemy group was Syrphidae (hoverfly) larvae ($n=182$). In June 2021, during peak *D. plantaginea* abundance, 150 Syrphidae were observed. The mean number of Syrphidae was 2 and 1 (SD = 3 and 2) per aphid-infested tree in flower margin and control orchards respectively. There was no significant effect of treatment, or distance from the orchard edge, on Syrphidae abundance on trees ($\chi^2=0.022$, df = 1, $p>0.05$ and $\chi^2=0.121$, df = 1, $p>0.05$, respectively) or the likelihood of Syrphidae presence on trees ($\chi^2=0.658$, df = 1, $p>0.05$ and $\chi^2=0.0001$, df = 1, $p>0.05$, respectively). However, the likelihood of Syrphidae presence and abundance was significantly and positively associated with increased *D. plantaginea* abundance per tree ($\chi^2=28.391$, df = 1, $p<0.001$ and $\chi^2=7.541$, df = 1, $p<0.001$, respectively).

The third most abundant group was Coccinellidae (ladybird) larvae and adults ($n=137$). In June 2021, during peak *D. plantaginea* abundance, 116 Coccinellidae were recorded. There was 1 (SD = 3) Coccinellidae per tree in control orchards, and 1 (SD = 1)

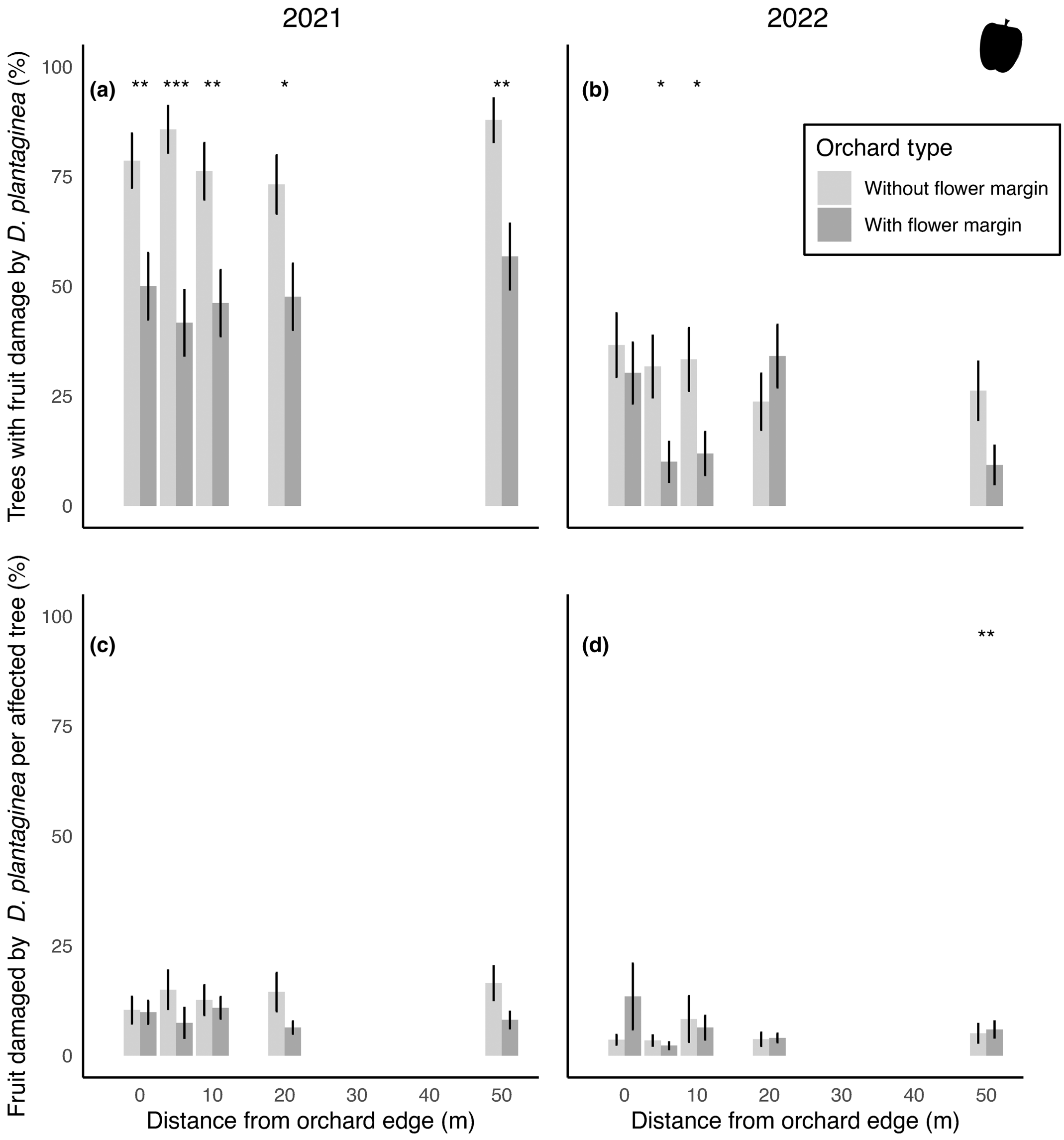

FIGURE 6 Mean percentage of trees with *Dysaphis plantaginea*-damaged apples in (a) 2021 and (b) 2022, and the number of *D. plantaginea*-damaged apples on trees with damage present in (c) 2021 and (d) 2022. Lines show standard error. Stars denote the significant effect of treatment at that distance from the orchard edge; $*p<0.05$, $**p<0.01$, $***p<0.001$.

every 3 trees in orchards with a flower margin. The likelihood of Coccinellidae presence was significantly and positively associated with increased *D. plantaginea* abundance per tree ($\chi^2=16.808$, df = 1, $p<0.01$). Additionally, there was a significant negative effect of increased distance from the orchard edge on the likelihood of coccinellid presence ($\chi^2=4.282$, df = 1, $p<0.05$), but there was no significant effect of flower margins on the likelihood of Coccinellidae presence ($\chi^2=0.983$, df = 1, $p>0.05$).

In 2021, 437 ants were found during *D. plantaginea* surveys. There was a significantly higher probability of Formicidae presence with increased *D. plantaginea* abundance ($\chi^2=21.851$, df = 1, $p>0.001$). There was a significant interactive effect of sampling round, and the presence of a flower margin on the number of trees with Formicidae present ($\chi^2=19.993$, df = 3, $p<0.001$). There were significantly fewer trees with ants present in flower margin compared with control orchards in April and July, but not in May or June (Figure 8, Table S4). Formicidae numbers were too low in 2022 for statistical analysis.

4 | DISCUSSION

4.1 | *Dysaphis plantaginea*

It is common for aphid pest pressure to vary widely by year as demonstrated in our study with 65% of trees infested in 2021 and 25% of trees infested in 2022. Senior et al. (2020) related the temporal variation in pests, at least in part, to changes in temperature and precipitation. For example, perhaps in this case the mild, wet winter proceeding the 2021 apple-growing season (Met Office, 2023) led to higher levels of infestation. Changes in pest numbers can both be caused by, and be a cause of, changes in the abundance of natural

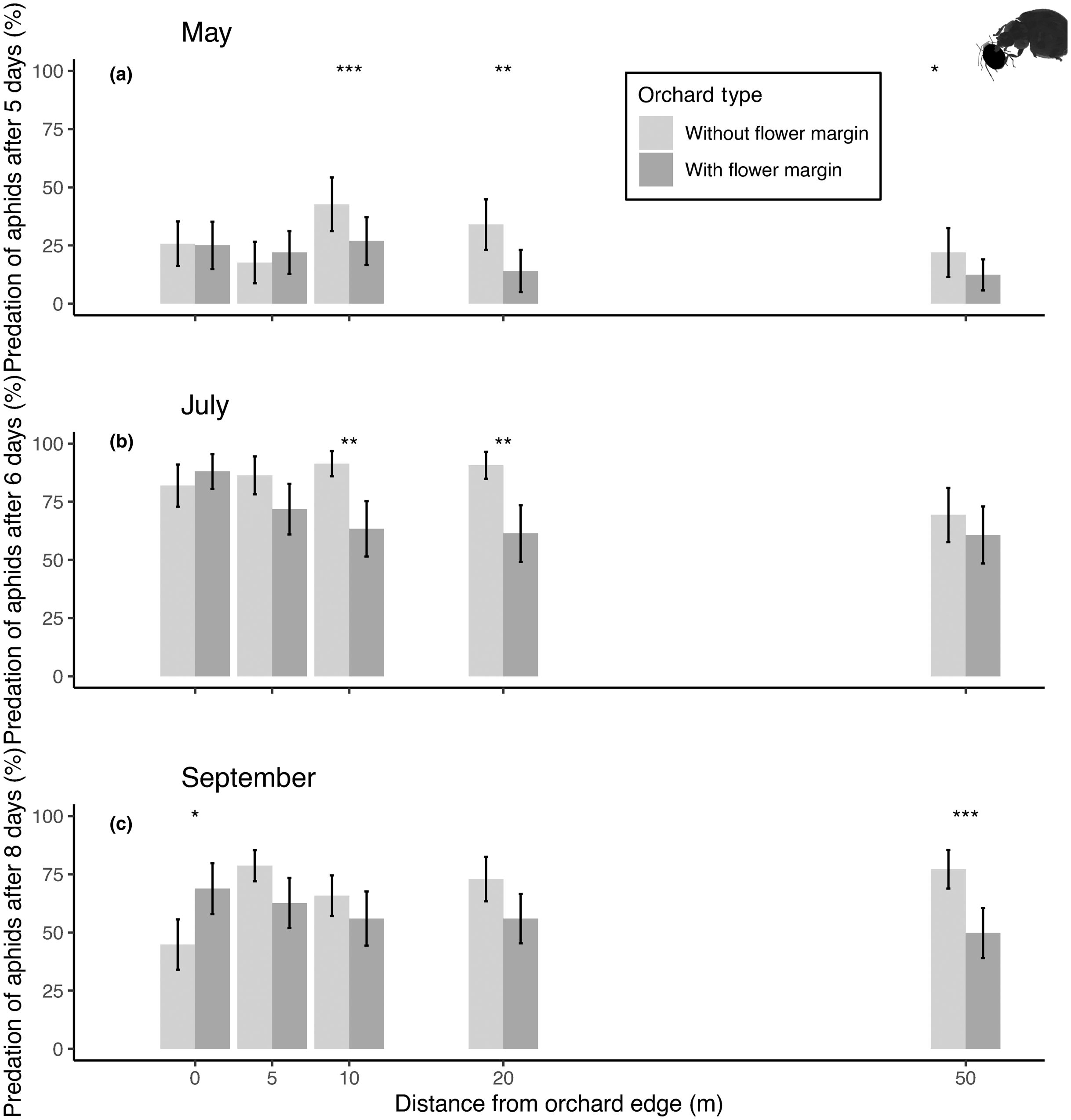

FIGURE 7 Depletion of aphids from bait cards in (a) May, (b) beginning of July and (c) beginning of September 2021. Lines show standard error. Stars denote the significant effect of treatment at that distance from the orchard edge; $^{*}p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$.

enemies, which might explain why there were double the number of trees with spiders in 2021 compared to 2022. While the abundance of *D. plantaginea* was too low in 2022 for detailed analysis, in 2021, a year with high levels of infestation, we found significantly fewer areas of the apple trees were infested with *D. plantaginea* in flower margin compared to control orchards. We also found a significant decrease in *D. plantaginea* abundance at 10 m from the orchard edge in flower margin orchards compared to 10 m in control orchards. Previous studies have provided some evidence that perennial flower strips can slow the growth of *D. plantaginea* colonies compared with control plots by increasing natural enemy populations (Cahenzli et al., 2019). The abundance, likelihood and duration of the presence of *D. plantaginea* can decrease with proximity to flower strips (Albert et al., 2017). The reduced number of areas of the apple trees infested by *D. plantaginea* in flower margin orchards would have reduced the number of buds or fruit clusters in close proximity to a colony. This could have reduced the likelihood of a tree having any damaged fruit at harvest since an aphid colony feeding on or near to buds and fruit is what causes fruit damage. As such, the reduced spread of aphid colonies in the trees could have been a driving factor behind the reduction in number of trees with damaged fruits. Of those infested trees, the number of damaged fruits was not significantly different in flower margin and treatment orchards, perhaps suggesting that there could have been a reduction in colony establishment rather than a difference in colony growth rates, although this was not directly measured.

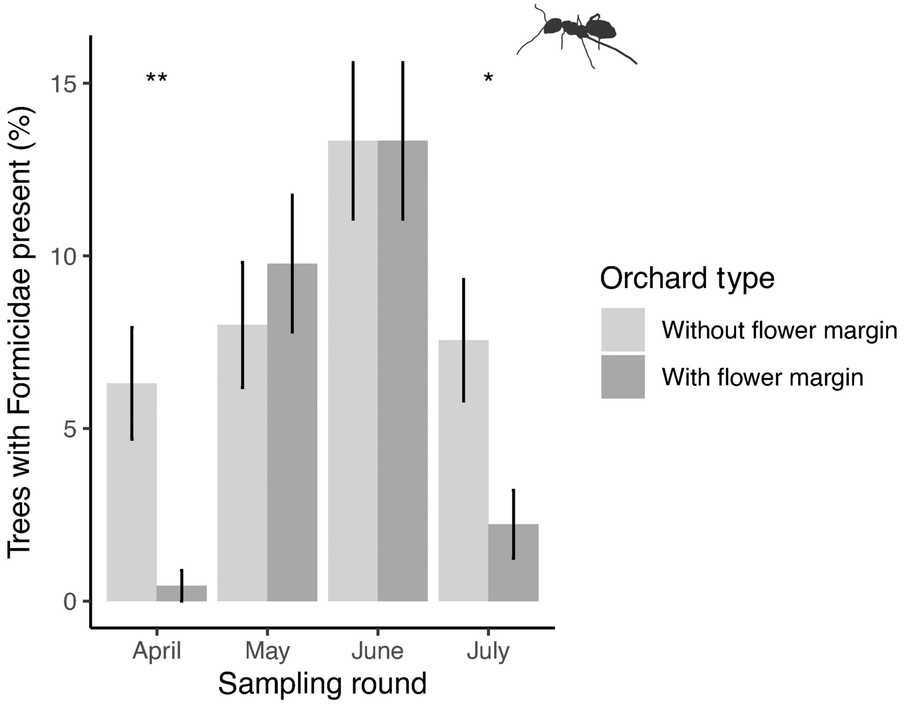

FIGURE 8 Percentage of orchard trees with Formicidae (ants) present in 2021. Lines show standard error. Stars denote the significant effect of the presence/absence of flower margins $*p < 0.05$, $**p < 0.01$.

4.2 | *Dysaphis plantaginea* fruit damage

During 2021 when there were high levels of *D. plantaginea* infestation, the proportion of trees with apple damage was significantly reduced, from 80% in control orchards compared to only 48% of trees in flower margin orchards. Assuming that 4.1% and 11.1% of the fruit was damaged by *D. plantaginea* on affected trees in the flower margin and control orchards respectively, and a marketable apple yield of 35,000 kg/ha for Gala orchards in the UK in 2021 (DEFRA (Department for Environment, Food, & Rural Affairs), 2023), the flower margins could result in an additional 2420 kg/ha of undamaged fruit (Table S6). To our knowledge, this is the first study to find a significant reduction in incidence of fruit damage at harvest in orchards provisioned with flower margins compared with control orchards. Only a few studies have investigated the effects of flower strips on fruit damage by *D. plantaginea*. For example, Campbell et al. (2017) measured the effect of flower margins in apple orchards and found no impact on yield, despite finding positive effects on natural enemy communities, as did Jacobsen et al. (2022). Similarly, a large-scale pan-European study found reductions in fruit damage by *D. plantaginea* after the second fruit drop, but not at harvest, perhaps due to quality thinning practices (Cahenzli et al., 2019). These studies assessed newly established flower strips (although Jacobsen et al. replaced 5-year-old, less-diverse strips). A review by Herz et al. (2019) indicated that older flower strips may be more effective, as in other crops (Blaauw & Isaacs, 2015), although, in apple orchards, only a minority of previous studies have investigated well-established strips (Albert et al., 2017; Cahenzli et al., 2017, 2019). In a recent agroforestry study in a farm without thinning practices, using 6-year-old sown flower strips, there was a reduced percentage of apples lost to *D. plantaginea* for trees with spontaneous flowering understories compared with both mown herbage and arable crop (Staton et al., 2021). In our study, and that of Staton et al. (2021), perhaps the maturity of the flower strips led to more effective reduction of fruit damage caused by *D. plantaginea*. Our observation in this study that wildflower margins significantly reduce the incidence of fruit damage at harvest in orchards, compared to control orchards, raises useful opportunities for orchard managers. It suggests that flower margins can help to control crop damage in the face of varying pest pressure resulting from crop management and climate variation. To our knowledge, this is the first study to demonstrate reduced *D. plantaginea* damage in conventionally managed fruit orchards with floral margins. A similar study in conventional orchards found no effect of inter-row flower strips on pest regulation services, which was suggested to be due to detrimental impacts on natural enemies by the plant protection products which were used at the time (McKerchar et al., 2020). To put fruit damage results into a financial context relevant for growers, future studies could investigate the economic significance of fruit damage and perhaps the net economic benefits of flower strips as a tool for pest suppression. Whilst this study focuses on *D. plantaginea*, there are many other insect pests of apple which have the potential to be controlled by natural enemies, for example, tortricids or codling moth (Bostanian et al., 2004; Fountain, 2022).

4.3 | Spill-over of *Dysaphis plantaginea* control

During 2021, when there were high levels of *D. plantaginea* infestation, spill-over of beneficial effects of flower margins, that is, reduced spread and fruit damage by *D. plantaginea*, reached up to 50m from the orchard edge, which was the maximum distance measured. By contrast, in 2022, with low levels of infestation, the positive impact of the flower margin was detected up to 10m away from the orchard edge. To find a significant effect on the incidence of fruit damage from marginal flower strips up to 50m into apple orchards suggests that mobile predators are key drivers of aphid control. For example, aphidophagous hoverflies can travel 50–250m from a pollen source (Harwood et al., 1994; Wratten et al., 2003), and Miliczky and Horton (2005) report that flower margins could affect the abundance of natural enemies up to 40m into orchards. The exact extent of the effect in any particular year is also likely to be affected by climate and crop management (Fountain, 2022). The average length of our orchards, perpendicular to the flower margin, was 130m. As such, our finding that the incidence of trees with fruit damage can be significantly, and consistently, reduced up to 50m away and nearing the centre of our orchards indicates that for *D. plantaginea* control, flower margins may offer a practical alternative to inter-row flower strips, which may interfere with farm machinery.

4.4 | Predators

The most abundant specialist predator groups found in *D. plantaginea* surveys were Syrphidae, and Coccinellidae, consistent with many previous studies (Albert et al., 2017; Cahenzli et al., 2019; Rodríguez-Gasol et al., 2019; Santos et al., 2018). However, we found no effects of flower margins on abundance or likelihood of presence for either group, suggesting that they are highly motivated to search for and attack *D. plantaginea* colonies. Other studies have generally found similar or neutral effects of flower strips (Jacobsen et al., 2022; Santos et al., 2018), or found a significantly increased abundance of generalists, and specialist predators including Syrphidae and Chrysopidae (Albert et al., 2017; Cahenzli et al., 2019). These authors also identified an increased likelihood of Syrphidae and Coccinellidae within *D. plantaginea* colonies on orchard trees where flower strips were provided (Albert et al., 2017). Jacobsen et al. (2022) found no difference in the proportion of aphid colonies containing predators during visual searches for *D. plantaginea* between orchards with and without flower strips. We found that Coccinellidae abundance and likelihood of Syrphidae presence on trees increased with higher abundance of *D. plantaginea* on trees, as was found by Albert et al. (2017). Natural enemies frequently aggregate in areas of high prey abundance. For specialist predators of aphids such as Syrphidae, Coccinellidae and Chrysopidae, it is not surprising that there is a positive response to aphid abundance (Albert et al., 2017; Cahenzli et al., 2019; Miñarro et al., 2005). Some hoverfly species are aphid density-dependent, that is, they lay more eggs where there is an increased size of aphid colonies (Graham, 1989), to meet the needs of their larvae. For example, *Episyrphus balteatus*, considered an important enemy of *D. plantaginea* (Dib et al., 2010), exhibits highly density-dependent egg-laying compared with other aphid predators (Sutherland et al., 2001). This species also avoids laying eggs in proximity to conspecific eggs, mummified aphids, other predators (Dib et al., 2011) or attending ants (Nagy et al., 2015). Perhaps, in our study, these behaviours masked the effects of flower margins on Syrphidae and their pest control services. Visual searches as a survey method could be less effective at recording faster-moving predators, for example, predatory Hemiptera. To sample these groups, a method such as tap sampling would reduce the opportunity for these predators to flee upon any disruption of the tree branches or leaves. Tap sampling however does not allow for the curled leaves surrounding a *D. plantaginea* colony to be uncurled.

There were significantly fewer trees with ants present in the flower margin compared to control orchards in April and July 2021. Ants prefer to obtain sugar from floral resources when aphid colonies are small, but as colonies grow and produce more honeydew, ants attend aphids protecting them from predators in exchange for the sugar (Katayama et al., 2013) resulting in aphid populations growing more rapidly due to reduced predator pressure (Nagy et al., 2015; Stewart-Jones et al., 2008). In our study, the reduction in ant presence in flower margin orchards, particularly early in the season, could have contributed to the reduced spread of infestation by *D. plantaginea* and reduced abundance at 10m in flower margin compared with 10m in control orchards. These results provide preliminary evidence to suggest that ant attendance may be reduced by a flower margin in the early and late seasons, which should be investigated further. Alternatively, it must also be considered that aphid infestation levels could be driving ant abundance.

4.5 | Predation

Although we demonstrated reduced *D. plantaginea* pressure in flower margin orchards, more *A. pisum* aphids were removed by predators from bait cards in the control orchards. During the assessments, the following groups were observed feeding from the cards; Formicidae (ants), Heteroptera (bugs), Chrysopidae (lacewing) larvae, Coccinellidae (ladybird) larvae and adult midges. Bait cards were used as a proxy for predation, and are particularly useful when there are time, resource or logistical limitations associated with the use of more elaborate methods of recording predation of live animals (Boetzl et al., 2020). Cahenzli et al. (2019) also found no significant increase in the activity of natural enemies, using aphid bait cards in flower strips compared to control orchards. Nevertheless, predation from bait cards was increased up to 55% in conventional apple orchards with flower strips as compared with control orchards in similar experiments by Campbell et al. (2017), despite finding no effects on aphid densities or natural enemies. Perhaps this was because sterilised moth eggs were used as bait instead of dead aphids, or due to the difference in location (Herefordshire, SW England). Other issues with the bait cards include dead compared to live aphids and the use of a different species, both potentially changing the interaction with natural enemies. Additionally, this method is less likely to reflect predation by some groups, for example, Syrphidae larvae. Bait cards are suggested to provide a proxy for predation by generalists rather than specialists (Lövei & Ferrante, 2017), which could suggest that generalists are not the main group driving *D. plantaginea* control here, although this remains unknown.

4.6 | Parasitism

Only two *D. plantaginea* mummies were found during the sampling seasons. Similar studies have also reported absences or low levels of evidence of parasitism of *D. plantaginea* (Albert et al., 2017; Brown & Mathews, 2014; Miñarro et al., 2005). Parasitism rates can be higher in organic orchards (Dib et al., 2010; Rodríguez-Gasol et al., 2019), and insecticide-free orchards (Santos et al., 2018), but not in every case (Albert et al., 2017), and a lack of observed parasitism may be driven by the high sensitivity of parasitoid wasps to plant protection products (Albert et al., 2017).

5 | CONCLUSIONS

To our knowledge, ours is the first study to detect a reduction in crop pest damage at harvest when a flower strip is present compared with a control. This is one of few studies to investigate flower strips in conventionally managed crop. We found an agronomically significant reduction in crop damage and yield loss by a globally important pest at far-reaching distances into the crop area. The positive effects of flower margins were stronger and extended further into the crop during a year with higher pest pressure. We show perennial flower strips as a realistic tool to support pest control services for sustainable production in the future, for example by buffering the effects of pest pressure related to climate variation and change.

AUTHOR CONTRIBUTIONS

Charlotte Howard: conceptualization; formal analysis; writing—original draft; visualisation. Michelle T. Fountain: conceptualization; writing—review and editing; funding acquisition. Claire Brittain: conceptualization; writing—review and editing; funding acquisition. Paul J. Burgess: conceptualization; writing—review and editing; funding acquisition. Michael P. D. Garratt: conceptualization; writing—review and editing; supervision; funding acquisition.

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CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

Data available from the University of Reading Research Data Archive at https://doi.org/10.17864/1947.000525 (Howard, 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Site information for study orchards.

Table S2. Amount of perennial and grass seed mix used to establish flower margins in orchards 1-4 and 5 (kg/ha), and percentage species composition.

Figure S1. Strip of grass in between rows of apple orchard trees (i.e interrow area) (left), strip of grass surrounding the apple orchard (i.e. headland area) bordered by a windbreak hedge (centre), and apple orchard with a flower margin (right).

Table S3. Tukey adjusted multiple comparison of significant interactive terms of 2-part hurdle model showing the significance of differences between flower margin and control orchards: (A) Percentage of trees with fruit damage by rosy apple aphids (spread), and (B) Percentage of damaged apples on affected trees (severity).

Table S4. Tukey adjusted multiple comparison of significant interactive terms of presence/absence binomial model showing the significance of differences between flower margin and control orchards: Percentage of orchard trees with Formicidae (ants) present.

Table S5. Tukey adjusted multiple comparison of significant interactive terms in binomial models showing the significance of differences between flower margin and control orchards: Percentage of bait aphids eaten from cards 5 to 8 days after deployment.

Table S6. Calculation of approximate equivalent kg/ha difference according to differences in number of trees with apple damage and severity per tree.

Appendix A. Aerial images of study orchards (yellow), and flower margins (purple) in Kent, UK, taken from Google Earth.

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